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Using three pairs of competitive indices to test for changes in plant competition under different resource and disturbance levels

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Abstract

Questions: How do different resource and disturbance levels interact to affect competition? How do different indices of competition change the interpretation of how competition changes under different resource and disturbance conditions?

Location: Greenhouse, Thompson Rivers University, Kamloops, British Columbia, Canada.

Methods: Three pairs of indices that have been used to differentiate the predictions of Grime (CSR) and Tilman's (R^*) theories were used to assess competition on two species of temperate bunchgrass, (*Pseudorogeneria spicata* and *Festuca campestris*) grown in a greenhouse on stress and disturbance gradients. Stress was created by manipulating the amount of water (high, low) and concentration of nutrient solution (high, low) added to pots, while disturbance was created by clipping (clipped, unclipped) in a fully factorial design. Plants were grown individually or with a single neighbour. The three pairs of indices were: (1) absolute and relative competition; (2) competitive effect and response; and, (3) competitive importance and intensity.

Results: Absolute competition and competitive importance were the only indices responsive to the resource gradient, which supports CSR theory, and also the only ones to record an effect of disturbance on the strength of competition – under high resource conditions. The other indices showed few responses along the gradients, which supports R^* theory. Measures of competitive effect and response did not differentiate the two theories.

Conclusion: We show that some indices of competition show a decline with increased stress and disturbance, while other indices do not. Therefore, it is necessary to choose a competition index appropriate to the question being asked. Competitive importance and absolute competition were responsive to changes in stress and disturbance, while the other indices were not.

Keywords: Absolute and relative competition; Clipping; Competitive effect and response; CSR strategy theory; Drought; *Festuca campestris*; Importance and intensity of competition; Nutrient availability; *Pseudoroegneria spicata*; R^* theory.

Nomenclature: Douglas et al. (1994).

Abbreviations: C_{ab} = absolute competition; C_{int} = competitive intensity; C_{imp} = competitive importance; C_e = competitive effect; C_r = competitive response.

Introduction

Competition is an important factor that structures plant communities (Tilman 1988; Grime 2001; Keddy 2001), but there are conflicting predictions as to how important it is depending upon the productivity of the habitat (Grime 1977; Tilman 1985; Thompson 1987; Grace 1995; Craine 2005). The two predominant arguments are CSR Strategy theory, stating that competition increases with productivity (Grime 1977); and, R^* theory (Resource-ratio hypothesis) that states competition is consistent along the productivity gradient but switches from below ground for water and nutrients to above ground for light as belowground resources become more available (Tilman 1982, 1988). It has been suggested that the difference between these two theories is semantic rather than of disparate ecological understanding (Welden & Slauson 1986; Grace 1991; Brooker et al. 2005) and even that the debate is unnecessary because the concepts of competition intensity and competition importance distinguish the two theories (Brooker & Kikvidze 2008). Evidence to support these two theories has been divided and perhaps limited (Goldberg et al. 1999; Wilson & Lee 2000; Miller et al. 2005, 2007; Wilson et al. 2007); support for either theory can change depending on which index is used to measure competition (Turkington

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et al. 1993; Grace 1995), and there are many (Weigelt & Jolliffe 2003).

It is important to have a clear understanding of how competition might be affected by productivity, especially because both theories impact current understanding of biodiversity. For example, CSR Strategy theory and R* theory both predict a hump-shaped relationship between species richness and productivity (Tilman 1982; Grime 2001). Neither CSR theory nor R* theory examine competition as a process in isolation. CSR theory examines the outcome of competition as a trade-off between competitive, ruderal and stress-tolerant plant strategies. Similarly, R* theory is based on a competition model, but resource availability is determined by other processes such as loss-rate (disturbance). Furthermore, while CSR and R* theories predict how the level of disturbance and stress will affect competition, these are generally not included in tests of competition.

There are many measures of competition (Weigelt & Jolliffe 2003), but three sets of measures have been used to explain and differentiate the sometimes conflicting predictions of CSR and R* theory: absolute and relative competition (Campbell & Grime 1992; Turkington et al. 1993; Grace 1995; Wilson & Tilman 1995), effect and response competition (Goldberg 1990, 1996; Goldberg & Landa 1991), and the importance and intensity of competition (Welden & Slauson 1986; Brooker et al. 2005). We will use the terminology above in an effort to reduce confusion resulting from the multiple names that have been associated with similar formulas (Table 1) (Weigelt & Jolliffe 2003).

Absolute and relative competitive ability have been shown to support both the theories of Grime and Tilman respectively (Campbell & Grime 1992; Grace 1993; Turkington et al. 1993). Absolute competition is estimated as reduction in biomass due to neighbours and should therefore decline with productivity, while relative competition is standardized by biomass production in the absence of competition and is more likely to remain constant along a productivity gradient (Goldberg & Scheiner 1993; Grace 1995).

Competitive effect and response have also been suggested to differentiate the two theories. Competitive effect is the ability of a plant to suppress its neighbours and correlates with plant traits such as growth rate which concurs with Grime's definition of competition (Goldberg 1990, 1996). Competitive response is the ability of a plant to withstand the effects of its neighbours, but it has not been so clearly linked to plant traits (Keddy et al. 1998; Cahill et al. 2005; Carlyle & Fraser 2006) and reflects Tilman's definition of a competitor – the species that can survive at the lowest resource availability (Goldberg 1990).

Finally, competitive importance and competitive intensity have been used to distinguish the two theories (Welden & Slauson 1986; Brooker & Kikvidze 2008). The importance of competition is a relative measure of the effect of competition at a point along the gradient relative to other processes and tends to support CSR theory; the intensity of competition is a relative measure of competition at a single point along the gradient and has been associated with R* theory (Brooker et al. 2005; Brooker & Kikvidze 2008). Only importance of competition can incorporate the role of other processes in describing the impact of competition – the importance of competition should decrease when other processes such as disturbance or stress are present. Given the association of absolute competition, competitive effect and competitive importance with

Table 1. Indices of competition compared in this experiment, including some citations of each indices' use and other names that have been used for the indices. In equations 1–5, T is the biomass of the target species and N is the biomass of the neighbour species. Competitors are either present (+) or absent (−). X and y are the greater and lesser, respectively, of T_+ and T_-. Max T_- for both species always occurred when the plant was grown under the high-water, high-nutrient condition without clipping and x was always equal to T_- (i.e., plants always had higher biomass when grown alone).

Index	Other names	Abbreviation, Equation	Citations
Absolute competition	Absolute competitive index (ACI)	$C_{ab} = T_- - T_+$	(1) Campbell & Grime (1992), Turkington et al. (1993), Grace (1995), Wilson & Tilman (1995)
Competitive intensity	Relative competitive index (RCI), relative neighbour effect	$C_{int} = T_- - T_+/x$	(2) Brooker et al. (2005), Grace (1995), Turkington et al. (1993), Campbell & Grime (1992), Wilson & Tilman (1995), Fraser & Miletti (2008), Markham & Chanway (1996)
Competitive effect		$C_e = 1 - N_+/N_-$	(3)
Competitive response	Relative yield	$C_r = T_+/T_-$	(4) Goldberg & Fleetwood (1987), Keddy et al. (1998), Fraser & Miletti (2008)
Competitive importance		$C_{imp} = (T_- - T_+)/(\text{Max } T_- - y)$	(5) Brooker et al. (2005)

CSR theory, these indices should predict an increase with increased productivity. In contrast, R* theory is based exclusively as a competitive model and thus under all conditions R* theory predicts that these measures will remain constant (Tilman 1982, 1988).

We conducted a factorial experiment to assess the role of competition between two grass species under combinations of stress (nutrient, water) and disturbance (clipping) treatments. We assessed the three sets of competitive indices under each combination of treatments to test if 1) the pairs of competitive indices differentiated the predictions of CSR and R* theory and 2) do the indices measure a decrease in the level of competition due to disturbance (loss-rate)? In addition, we tested if the results provided by different indices are consistent with predictions regarding how disturbance alone, and interacting with resources, affects competitive outcomes.

Materials and Methods

Study species

Pseudorogeneria spicata (Pursh) A. Love (bluebunch wheatgrass) and *Festuca campestris* Rydb. (rough fescue) are temperate bunchgrasses native to the southern interior of British Columbia, Canada. Both species occur along an elevation gradient with *P. spicata* tending to dominate in drier less productive elevations and *F. campestris* tending to dominate at wetter more productive elevations.

Experimental design

The experiment was done in the Research Greenhouse at the Thompson Rivers University Campus, Kamloops, British Columbia, Canada. Greenhouse conditions were electronically controlled for the duration of the experiment to maintain daytime conditions at 22°C and 60% relative humidity, and night-time conditions at 15°C and 85% relative humidity, which are within the range of local, natural growing season conditions. Supplemental lighting was supplied by three 1000 W halogen sulphide lamps in a 14:10 hour day: night cycle.

Seeds of *P. spicata* and *F. campestris* were collected from multiple locations in Lac du Bois Provincial Park, British Columbia, Canada (UTM 10 North 680737 5625980; 4 to 10 km north of Kamloops). After three months of cold storage, the seeds were placed in Petri dishes on a bed of damp sand to germinate. Seedlings with a radical at least 30 mm long were transplanted into 240 ml pots (6.4×6.4 cm opening, 4×4 cm base and 8.9 cm tall) containing clean sand saturated with 70 ml of Rorison's solution (Hendry & Grime 1993). After one week, dead seedlings were replaced with seedlings that had been planted individually in identical pots at the same time. All pots received a top watering of 50 ml Rorison's solution every five days and a bottom watering of distilled water when needed to maintain 5 mm of standing water for the first 21 days of the experiment. After 21 days the pots were subjected to their respective nutrient and watering treatments.

The four factors examined in this study (water, nutrients, clipping and competition) each had two levels. Each species was planted in either competition or not in competition, so there were 3 planting combinations: *P. spicata* alone, *R. fescue* alone, and both species together. All factors were combined for a total of 16 pot combinations for each species. Each combination was replicated 20 times in 4 blocks (5 replicates per block). Thus, our experiment had 480 pots (planting combinations (3) x water (2) x nutrients (2) x clipping (2) x replicates (20) = 480). All pots received 30 ml of Rorison's solution every 5 days. High nutrient treatments received regular strength Rorison's solution; low nutrient treatments received a 1/10 dilution. High water treatments received a bottom watering of distilled water as needed to maintain the pot sitting in 5 mm of water; low water treatment pots received the top watering of nutrients but did not receive any bottom watering. Plants that received the clipping treatment were clipped after 45 days to reduce their leaves by 75% length (Hendry & Grime 1993). Competition was created by placing an individual of both species of grass together in a pot; no competition treatments had a single individual in the pot. All plants were clipped at ground level 90 days after planting; the biomass was dried for 48 hours at 65°C and then weighed. Attempts to separate roots of the two species could not be done with certainty, so only aboveground measures of biomass were used to estimate the competition indices.

Competitive indices

The five competitive indices compared in this study were: absolute competition (C_{ab}), competitive intensity (C_{int}), competitive effect (C_e), competitive response (C_r) and competitive importance (C_{imp}) (Table 1). C_e, C_r, and C_{int} are essentially equivalent calculations. C_e is the effect of the target species on its neighbour while C_{int} is the effect of competition

on the target species from its neighbour, and because we are dealing with only two species, the calculation of C_{int} for *P. spicata* is identical information to the calculation of C_e for *F. campestris*, which is why only five indices are examined rather than six. Competitive response is equivalent to $1 - C_e$. We have included both calculations to help illustrate the different competition indices. These calculations would not necessarily be identical if a larger species set or community set were used. Each index was calculated for the each plant grown with a neighbour compared to the mean dry biomass of that species grown alone. Each index of competition was applied to all pots.

Data analysis

The effect of water treatments (high, low), nutrient treatments (high, low), clipping (clipped, unclipped) and block on the biomass was analysed separately for each species with an analysis of variance (ANOVA). Significant blocking effects in the final plant biomass caused us to calculate competitive measures on a block by block basis (i.e. competitive indices were calculated with target plants and plants grown without neighbours from within the same block). The effect of water treatments, nutrient treatments, clipping and block on each competitive index was analysed separately for each species. Block was not significant in the ANOVA of competitive indices and was not included in the final analyses; including block in the analyses did not change the interpretation of the analyses. All analyses were done using R version 2.7.0, R Development Core Team, R Foundation for Statistical Computing, Vienna 2008.

Results

Biomass

The biomass of both species was reduced by four of the treatments: low water, low nutrients, clipping and competition; however, the two species responded differently to treatment interactions (Table 2). *Pseudorogeneria spicata* had a decrease in biomass with decreasing resource availability but there was no difference in the final biomass between the high water – low nutrient and low water – low nutrient treatments (Fig. 1a). Under the high water – high nutrient conditions, clipping lowered biomass of *P. spicata*, and there was a clipping×competition interaction. *Festuca campestris* did not respond to any treatments when nutrients were low. Under high nutrient conditions the presence of the competitor had the largest effect. Clipping reduced the biomass of *F. campestris* only under the high water – high nutrient conditions (Fig. 1b).

Competitive indices

Absolute competition (Fig. 2e, j) declined with decreasing resource availability for both species. There was a significant three-way interaction between water, nutrients and clipping for C_{ab} for *F. campestris*; under the high-water high nutrient conditions clipping decreased C_{ab} (Table 3).

Table 2. Summary of four-way ANOVAs testing treatment effects on the above ground biomass of *Pseudorogeneria spicata* and *Festuca campestris*. Values in bold are significant ($P < 0.05$).

	df	*P. spicata* biomass		*F. campestris* biomass	
		F-value	*P*	*F*-value	*P*
Block	3	14.100	**<0.001**	2.181	0.090
Water	1	224.687	**<0.001**	54.564	**<0.001**
Nutrient	1	1012.28	**<0.001**	619.849	**<0.001**
Competition	1	15.084	**<0.001**	261.512	**<0.001**
Clipping	1	19.870	**<0.001**	33.291	**<0.001**
Water:Nutrient	1	150.567	**<0.001**	48.090	**<0.001**
Water:Competition	1	1.780	0.183	6.551	**0.011**
Water:Clipping	1	1.618	0.204	3.030	0.083
Nutrient:Competition	1	4.929	**0.027**	158.070	**<0.001**
Nutrient:Clipping	1	13.165	**<0.001**	14.907	**<0.001**
Competition:Clipping	1	0.099	0.753	0.645	0.423
Water:Nutrient:Competition	1	0.458	0.499	7.218	**0.008**
Water:Nutrient:Clipping	1	3.056	0.081	6.223	**0.013**
Water:Competition:Clipping	1	0.010	0.921	1.134	0.288
Nutrient:Competition:Clipping	1	0.123	0.725	0.680	0.410
Water:Nutrient:Competition:Clipping	1	0.070	0.791	2.390	0.123
Residuals		271		267	

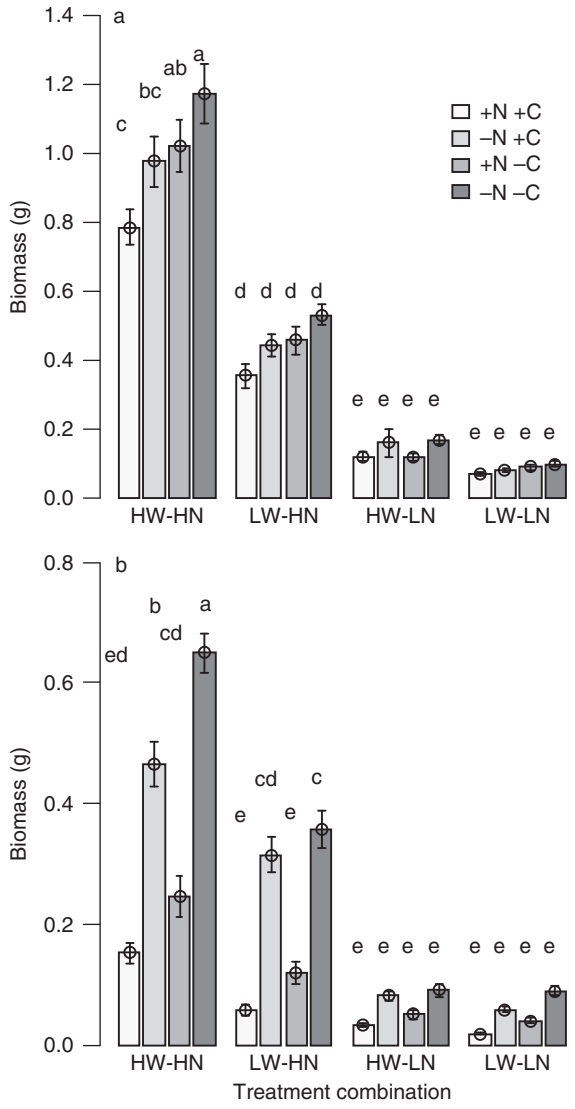

Fig. 1. Mean (± 1 SE) biomass of a) *Pseudorogeneria spicata* and b) *Festuca campestris* under all treatment combinations. On the x-axis, H and L refer to high and low water (W) and nutrients (N). Plants were either grown with (+N) or without (– N) a neighbour, clipped (+C) or unclipped (– C). Small case letters above the bars represent significant differences within water and nutrient treatment groups due to competition and clipping effects (Tukey HSD). Note the different range on the Y-axis for the two figures.

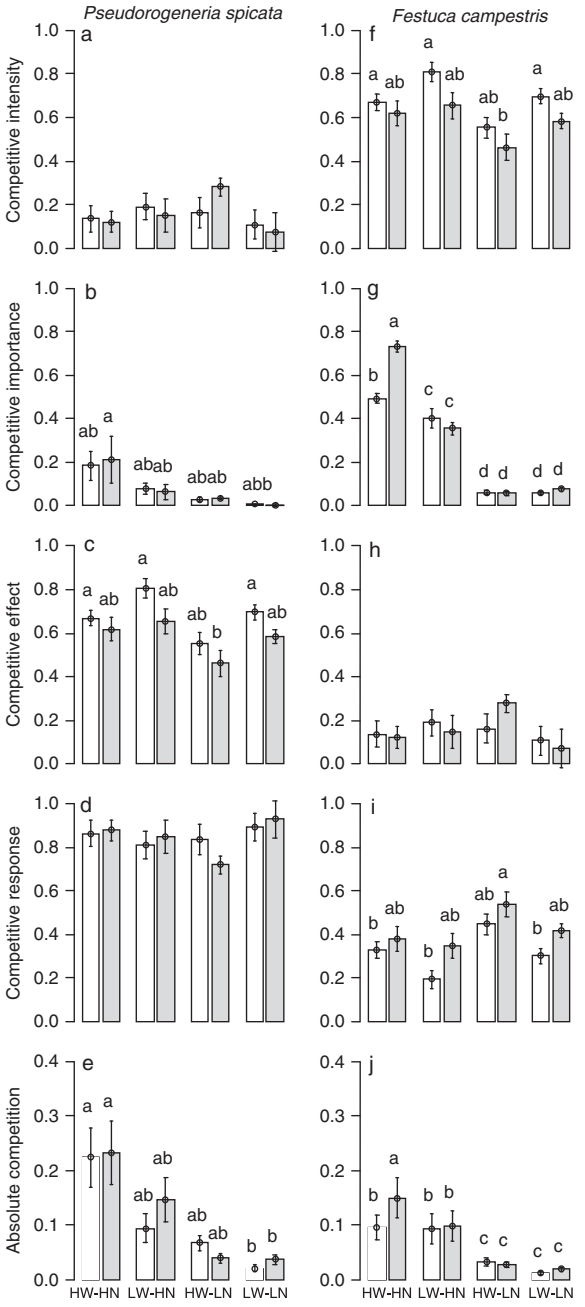

Fig. 2. The five competition indices (± 1 SE) for *Pseudorogeneria spicata* (a – e) and *Festuca campestris* (f–j) for all treatment combinations. Treatments are arranged from left to right in order of increasing nutrient and water stress. H and L refer to high and low water (W) and nutrients (N). Plants were clipped (open bars) or not clipped (shaded bars). Bars sharing the same letter (Tukey HSD) are not significantly different ($P = 0.05$); in figures with no letters there was no significant difference. Note the different range on the Y-axis for absolute competition (e and j).

Competitive intensity (or relative competition) was constant across all treatment combinations for *P. spicata* (Fig. 2a, Table 3). Nutrients, water and clipping all had significant effects on competitive intensity for *F. campestris* but not in a consistent manner (Fig. 2f, Table 3).

Similarly, the measures of C_r for *P. spicata* (Fig. 2d) and C_e for *F. campestris* (Fig. 2h) (both based on identical calculations) did not vary across treatments. However, C_e for *P. spicata* (Fig. 2c) and C_r of *F. campestris* (Fig. 2i) (also identical calculations), responded to water, nutrient and clipping

Table 3. Summary of three-way ANOVAs for *Pseudorogeneria spicata* and *Festuca campestris* across treatment combinations for all 5 measures of competition: Competitive intensity (C_{int}), competitive importance (C_{imp}), competitive effect (C_e), competitive response (C_r) and absolute competition (C_{ab}). Values in bold are significant ($P < 0.05$).

	df	C_{ab}		C_{int}		C_e		C_r		C_{imp}	
		F-value	*P*	*F*-value	*P*	*F*-value	*P*	*F*-value	*P*	*F*-value	*P*
P. spicata											
Water	1	0.543	**0.035**	1.456	0.230	9.594	**0.002**	1.456	0.230	4.758	**0.031**
Nutrient	1	15.576	**<0.001**	0.136	0.713	11.512	**<0.001**	0.136	0.713	13.175	**<0.001**
Clipping	1	0.003	0.955	0.123	0.726	8.194	**0.005**	0.123	0.726	0.030	0.864
Water:Nutrient	1	0.409	0.523	3.449	0.066	0.446	0.506	3.449	0.066	2.137	0.146
Water:Clipping	1	0.042	0.838	1.061	0.305	0.722	0.397	1.061	0.305	0.128	0.722
Nutrient:Clipping	1	0.036	0.851	0.683	0.410	0.007	0.936	0.683	0.410	0.011	0.916
Water:Nutrient:Clipping	1	0.000	0.995	0.460	0.499	0.326	0.569	0.460	0.499	0.076	0.783
Residuals	122										
F. campestris											
Water	1	11.630	**0.009**	9.594	**0.002**	1.456	0.230	9.594	**0.002**	56.569	**<0.001**
Nutrient	1	385.72	**<0.001**	11.512	**<0.001**	0.136	0.713	11.512	**<0.001**	1046.44	**<0.001**
Clipping	1	1.275	0.261	8.194	**0.005**	0.123	0.726	8.194	**0.005**	15.573	**<0.001**
Water:Nutrient	1	14.75	**<0.001**	0.446	0.506	3.449	0.066	0.446	0.506	75.841	**<0.001**
Water:Clipping	1	2.960	0.088	0.722	0.397	1.061	0.305	0.722	0.397	18.326	**<0.001**
Nutrient:Clipping	1	1.473	0.227	0.007	0.936	0.682	0.410	0.007	0.936	16.547	**<0.001**
Water:Nutrient:Clipping	1	6.314	**0.013**	0.326	0.569	0.459	0.499	0.326	0.569	30.416	**<0.001**
Residuals	122										

treatments but these were not consistent across treatments.

Competitive importance declined for both species with declining resources, although the trend was more pronounced for *F. campestris* (Fig. 2b, g). Additionally, C_{imp} was reduced for *F. campestris* under the high water treatment×clipping, and all possible interactions were significant (Table 3).

Discussion

We have shown that resource availability interacts with disturbance to affect competition but it depends on the index used. Others have shown that the index used to assess competition can influence how we interpret the effects of competition under changing resource availability (Campbell & Grime 1992; Turkington et al. 1993; Grace 1995; Wilson & Tilman 1995; Brooker et al. 2005). Two pairs of indices, competitive importance – competitive intensity, and absolute competition – relative competition, distinguished CSR and R* theory along resource and disturbance gradients, while the competitive effect – competitive response pair of indices did not.

Interacting effects on biomass

Effects of treatments on biomass production were as expected; clipping, low water, low nutrients and competition individually lowered the biomass of each species. However, additive effects of combinations of treatments tended to decrease biomass production more than any single treatment. Furthermore, the biomass response by the two species varied due to treatment interactions.

Dominance is important when interpreting the results of competition experiments because the effects of competition may be less apparent in dominant species than in subordinates (Goldberg 1987; Schwinning & Weiner 1998). Competitive ability has been positively correlated with plant size (Gaudet and Keddy 1988) and growth rate (Grime 2001). *Pseudorogeneria spicata* is the larger species (Fig. 1) and also has a faster relative growth rate than *F. campestris*, (from 2 to 21 days: $0.49\,g \cdot g \cdot day^{-1}$ and $0.22\,g \cdot g \cdot day^{-1}$ respectively, C.N.Carlyle unpublished data), suggesting that *P. spicata* is the better competitor and dominant species. This is an important consideration when interpreting the results of this experiment because *P. spicata* was less affected by treatments than *F. campestris* (Table 2).

Pseudoroegneria spicata only experienced significant biomass reductions when both clipping and competition were present, and when in high resource conditions; similar effects were apparent in a field study examining both drought and clipping on *P. spicata* (Busso et al. 1990). However, when grown in competition with *Centaurea maculosa, P. spicata* exhibited facilitative effects from the presence of the neighbour, but total foliage was reduced by increasing clipping severity (Kennett et al. 1992). At the end of our study, the effects of clipping were not apparent on the biomass production of *P. spicata*, except

in the high water-high nutrient treatment, but it is likely that a more severe clipping treatment, created by either increasing the amount of biomass removed or subjecting the plant to multiple clippings, would have produced more significant reductions in plant biomass as has been observed in a field study with this grass (Arredondo & Johnson 1998). The resistance of *F. campestris* to clipping, in all but the high resource, competition-free case, is inconsistent with field experiments (Willms & Fraser 1992; Vujnovic et al. 2000), but again our clipping regime on comparatively younger plants may not have been severe enough to induce a response. However, this does suggest ability by both of these species to compensate for the effects of clipping and that the effect of clipping is reduced as conditions become more stressful.

Comparing the pairs of competitive indices

Resource availability (*i.e.* productivity or stress) and disturbance have long been recognized to influence measures of competition and structure communities, but with only a few exceptions resources have dominated research questions and the interaction of the two processes examined less frequently (but see Campbell & Grime 1992; Turkington et al. 1993). However, because indices of competition have generally been designed to examine the influence of a neighbour they can still be applied to a range of environmental conditions that includes interactions (but see Goldberg & Scheiner 1993; Grace 1995) to test the consistency of methods examining changes in competition.

Absolute competition and relative competition

In general, C_{ab} supports the predictions of CSR theory, and C_{int} supports the predictions of R^* theory. Absolute competitive indices and relative competitive indices (C_{int}) have been extensively compared and reviewed in the long debate examining how competition changes along productivity gradients and their advantages and disadvantages have been discussed (see Goldberg & Scheiner 1993; Grace 1995; Miller 1996; Oksanen et al. 2006). These indices have also been criticised for their inability to account for changes in plant size that will occur in different environments (Wilson 2007). Absolute competition is expected to show a decline with resource availability because the actual amount of biomass produced under low resource conditions is less; this is consistent with previous studies examining these indexes along resource gradients (Campbell & Grime 1992; Turkington et al. 1993; Wilson & Tilman 1995). These observations are consistent with CSR theory, where one process should decline when other processes are also present. Clipping did not have a consistent effect on C_{int}, but it did lower the measure of absolute competition for *F. campestris* under the high resource treatment, which suggests that under some circumstances clipping can influence C_{int}.

Our results concur with field studies that examined these two indices of competition. C_{ab} increased with increasing resource availability and declining disturbance (Campbell & Grime 1992), while C_{int} did not change along a productivity disturbance gradient (Wilson & Tilman 1995). Turkington et al. (1993) applied both C_{ab} and C_{int} along a productivity-disturbance gradient and showed that C_{ab} supported CSR theory while relative measures of competition supported R^* theory. The application of C_{int} and C_{ab} in tundra communities with different productivity levels showed that competition decreased when herbivory was present in lower productivity sites but with no difference in competition between sites of differing productivity(Olofsson et al. 2002). C_{ab} responded to both disturbance and productivity while C_{int} was generally consistent along both gradients in a manner similar to C_r and C_e which is due to the identical calculations used to measure these concepts of competition.

Competitive effect and competitive response

Contrary to Goldberg's (1990) assertion, C_e and C_r did not differentiate the two theories; neither measure decreased with lowered resource availability although the C_e of *P. spicata* on *F. campestris* and the C_r of *F. campestris* showed some variation among the treatment combinations.

Diffuse competition (a variant of competitive intensity and competitive effect) measured along a lake shore increased with both lower disturbance (wave action) and higher productivity (Wilson & Keddy 1986). A negative relationship between C_e and stress and a positive relationship between C_r and stress was found when eight species of wetland plants were examined along a water depth gradient, suggesting support of CSR theory for both measures of competition (Fraser & Miletti 2008). When root and shoot competition were measured separately using a natural log of competitive response no change in competition was observed above or below ground (Cahill 2002). Defining competitive response has been especially problematic but the solution

may require a trait-based approach (Keddy et al. 1998; Cahill et al. 2005; Carlyle & Fraser 2006). Conflicting findings for the response of these measures suggest that further investigation is required to determine the relationship between C_e and C_r.

There is a logical inconsistency in the way different indices have been used to describe the two theories. C_e has been associated with CSR theory, and C_{int} with R^* theory, but both measures of competition use the same formula in their calculation. We found that neither C_e nor C_{int} declined with decreasing resource availability, hence these two measures should both concur with R^* theory. Additionally, the formula commonly used to calculate C_r (Table 1 equation 3) is the inverse of C_e (Table 1 equation 1), so it is impossible for these two equations to show different trends in the strength of competition. We used calculations of competitive effect and response that differed from the original calculations using regression methods applied over a range of competitor densities (Goldberg & Werner 1983; Goldberg & Fleetwood 1987). The equations we used in this study have been commonly used to calculate C_e and C_r (Table 1) and while these are still useful concepts these equations should be used with caution when investigating competitive effect and response relationships.

Competitive intensity and competitive importance

Competitive importance and competitive intensity differentiated the two theories; representing CSR and R^* theories respectively. The pattern of C_{int} along the gradients has already been discussed because, as pointed out earlier, C_{int} is identical to C_e and it was already paired with C_{ab} as "relative competitive intensity". C_{imp} showed a distinct decline with reduced resource availability for *F. campestris*; the importance of competition was greatest when resources were most available. The trend is also apparent for *P. spicata* but only significant between the extremes of resource availability when unclipped. This was not surprising because biomass production by *P. spicata* was not reduced by the presence of a competitor.

These results agree with those reported by Brooker et al. (2005), where C_{imp} declined with standing biomass but C_{int} did not. In a comparison of three plant species C_{imp} decreased with fertility but it was suggested that competitive importance was dependent on the ability of the species to tolerate low resource availability (Gaucherand et al. 2006). Sammul et al. (2000), using a different calculation of competitive importance, reported a correlation between both C_{int} and C_{imp} when competition was calculated using the number of shoots rather than biomass, and Welden et al. (1988) detected no relationship between importance or intensity and a water stress gradient for desert shrubs. We observed a reduction in competitive importance due to clipping under the high resource conditions for *F. campestris*, which further supports arguments that competition in CSR theory is best measured with this index because the measure of competition declines when additional processes are in place. We are unaware of any other study that explicitly tests changes in C_{imp} due to disturbance; however, our findings suggest that C_{imp} concurs with the predictions of CSR strategy theory. Recalculating C_{imp} on existing data sets might confirm if this result is more common.

We have also provided further evidence that a contributing factor to the long debate of how competition changes along a productivity gradient is the use of competitive indices. In our study, two of the pairs of indices can lead to different conclusions depending on which index is selected. Studies of plant competition should use more than one index when reporting results. In our study C_e and C_r lead to the same conclusion, thus these indexes should not be used in contrast. C_{int} pairs against both C_{ab} and C_{imp}, but C_{ab} is more likely to show changes along a productivity gradient (Grace 1995). Thus, we suggest reporting both C_{imp} and C_{int} together.

Our study used a simple system, only one or two plants growing in a single pot, but ultimately ecologists are interested in the plant-plant interactions that structure natural communities. Indexes of competition have been criticised for not addressing community-level responses over longer periods of time (Frekelton et al. 2009). Pairwise competition experiments provide a controlled setting in which to investigate the mechanism of plant interactions even though they do not always reflect field distributions (Engel & Weltzin 2008). This problem is particularly evident in the competitive effect and response pair of indices which, in a pairwise experiment, will provide identical results.

Disturbance decreased C_{ab} and C_{imp} under high resource conditions. While this result has ecological significance it also creates an important consideration when testing for changes in competition along productivity gradients. If disturbance is not controlled it would be possible to reject the hypothesis that competition declines with productivity if disturbance processes reduce competition at high productivity while having no impact at low productivity, essentially creating equal measures of

competition at both high and low productivity. Disturbance effects on competition should be accounted for, especially in field experiments, where it may be difficult to determine the extent of disturbance.

Conclusions

Levels of stress *and* disturbance can alter competition indices. C_{imp} and C_{ab} declined with decreasing resource availability and were also reduced by disturbance thus supporting their association with CSR theory. C_r and C_{int} did not decline with resources or clipping in a manner consistent with CSR theory and were generally unchanged along both gradients, confirming their association with R^* theory. C_e, which has been associated with CSR theory did not decline along either gradient, and given that it is obtained with a calculation similar to C_r and C_{int} suggests that the calculation of C_e used here does not correspond to CSR theory. Relative measures of competition, such as C_e, C_r and C_{int}, are indexed and thus reduce the likelihood of observing change along stress or disturbance gradients. We encourage careful consideration when selecting and using competition indices and suggest the use of multiple indices when testing for differences in competition in different environments.

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